

Bison bison. By Mary Meagher

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Bison (Hamilton-Smith, 1827)

Bison Hamilton-Smith, 1827:373. Type species *Bison bison* (Linnaeus, 1758). Proposed as subgenus, recognized as genus by Knight, 1849:408.

CONTEXT AND CONTENT. Order Artiodactyla, Family Bovidae, Tribe Bovini. The genus *Bison* includes two extant species, *B. bonasus*, the European bison or wisent, and *B. bison*, the late Holocene bison of North America.

Bison bison (Linnaeus, 1758)

Bison

Bos bison Linnaeus, 1758:72. Type locality earlier considered to be "Mexico" (Thomas, 1911); subsequently considered to be the "Quivira Region," (central Kansas; Hershkovitz, 1957); redesignated as the Canadian River Valley of eastern New Mexico, United States (McDonald, 1981).

Bison americanus Brisson, 1762:56. Type locality America.

Bison occidentalis Lucas, 1898:678. Type locality Fort Yukon, Alaska.

Bison sylvestris Hay, 1915:515. Type locality Huron Co., Ohio.

Bison bison Jordan, 1888:337. First use of present name combination.

CONTEXT AND CONTENT. Context as given above. Two subspecies are recognized (McDonald, 1981; Skinner and Kaisen, 1947). Synonymy for both subspecies follows Skinner and Kaisen (1947):

B. b. athabasca Rhoads, 1897:498. Type locality, within 50 miles southwest of Fort Resolution, Mackenzie District, Northwest Territories, Canada (*occidentalis* Lucas, *oregonus* Bailey, and *haningtoni* Figgins are synonyms).

B. b. bison (Linnaeus, 1758). Type locality, see above (*americanus* Brisson, *sylvestris* Hay, *pennsylvanicus* Shoemaker, and *septentrionalis* Figgins are synonyms).

DIAGNOSIS. The following applies to the genus and species: horn cores in cross section at the base more or less triangular (males) or elliptical to circular (females), cores extend outward laterally from frontals forward of the occipital plane; frontals quadrate, flat to convex between the horn cores, never bossed; parietals on or about the same plane as the frontals, parietal plane forming an obtuse angle with occipital plane; occipital broad; orbits tubular (more so in males), protruding anterolaterally; nasals broad, short, triangular; premaxilla triangular, nasal process of premaxilla not reaching nasals (Figs. 1 and 2). *B. bison* includes specimens dating 5,000 BP and less (McDonald, 1981; Wilson, 1975).

GENERAL CHARACTERS. The body is massive, tall but proportionately narrow in transverse profile (Fig. 3). Both massiveness and height are accentuated by the shoulder hump formed by elongation of the neural processes of thoracic vertebrae and musculature of the shoulder and thoracic girdle. The hindquarters are lighter than the frontquarters; this disproportion is further accentuated by marked pelage differences between front and rear. Pelage is brown, long over the forehead, neck, hump, and frontquarters, short over the rear and tail. The tail is relatively short, with tufted tip. The head is large and carried low on the short, thick neck. Both sexes have short, black horns that curve upward and inward and taper to a circular, relatively sharp tip. Eyes are placed anterolaterally; ears are well buried in the long pelage of the head. The legs are relatively short and stout. Hooves are black with a nearly circular print.

Sexes are dimorphic with females similar to males but generally presenting a smaller, slighter appearance (Fig. 3). External

measurements (in mm) for males and females, respectively (Hall, 1981; Meagher, 1973; Seton, 1929), are: total length, 3,040 to 3,800, 2,130 to 3,180; tail length, 330 to 910, 300 to 510; hindfoot, 580 to 680, 500 to 530; height at shoulder, 1,670 to 1,860, 1,520 to 1,570; body mass (in kg), 544 to 907, 318 to 545. Maximum recorded mass is 1,724 kg for a semidomestic bull (Hebbring, 1978). Males are about 9.1% heavier than females of equal girth (Kelsall et al., 1978). Males have proportionately stouter, more evenly curving horns, with horn cores burred at the base. Their hump structure is much larger and the neck is relatively stouter. They have longer pelage on the forehead, chin, ventral mane, and chaps of the forelegs, and a more pronounced line of demarcation between the longer hair of the forequarters and the shorter hair of flanks and rear.

B. b. athabasca and *B. b. bison* closely resemble each other.

B. b. athabasca is generally larger but there is overlap. Selected measurements (in mm) of male skulls for *B. b. athabasca* and *B. b. bison*, respectively (McDonald, 1981), are as follows: maximum length, 562 to 604, 500 to 583; spread of horn cores, 542 to 848, 510 to 778; least width at frontals between horn cores and orbits, 273 to 313, 237 to 318.

DISTRIBUTION. Bison formerly were widespread in North America from Alaska and western Canada across the United States and into northern Mexico (Fig. 4). Occupation of marginal areas may have been intermittent (McDonald, 1981). McDonald (1981) believes the maximum geographic distribution of *B. b. bison* occurred in the late prehistoric period because of the many historical accounts of bison presence near the margins of the indicated maximum range (Christman, 1971; Reed, 1955; Roe, 1970; Rostland, 1960). The distribution of *B. b. athabasca* is less well known (McDonald, 1981). They apparently disappeared from Alaska before historic times but there are unfossilized specimens (Skinner and Kaisen, 1947).

Today bison occur as geographically isolated population units in parks, preserves, and other public lands, and on private ranches and small holdings throughout and external to the maximum known geographic distribution (Fig. 4). Major free-ranging populations occur in Canada (Mackenzie Sanctuary, Wood Buffalo National Park and adjacent Slave River lowlands) and the United States (Yellowstone National Park); a few smaller units also exist (Reynolds et al., 1982).

Altitude does not appear to have limited bison distribution. Evidence of past bison occupation was reported from about 3,903 m in Colorado (Beidelman, 1955), from 2,897 m to about 3,659 m in Wyoming (Fryxell, 1928), and at approximately 3,200 m in Montana (Pattie and Verbeek, 1967).

FOSSIL RECORD. Although the time and place of origin of the ancestors of *B. bison* are obscure, the earliest dated remains of the genus occur from the late Pliocene of Central Asia, with possible early Pleistocene occurrences from northern India and northern China (McDonald, 1981). Bison seemingly were confined to temperate and upland east Asia until after the early Pleistocene. Thereafter they appeared in southeastern and central Europe, becoming relatively common as fossils and in later cave paintings throughout much of Europe. Bison reached northern Eurasia during the middle Pleistocene and spread across the Palearctic into Alaska, but survived in northern Eurasia until the very late Pleistocene (McDonald, 1981). They first appeared in the fossil record south of Beringia in North America in early late Pleistocene faunas (Guthrie, 1980; McDonald, 1981). Most specimens of bison are known from the late Pleistocene of North America and higher latitude Eurasia, and the Holocene steppes and adjacent forests of Eurasia and North America (McDonald, 1981).

The evolutionary line leading to *B. bison* remains controversial although there seems to be general agreement on many elements. *Proleptobos* from the early Pliocene may be the ancestor of the



FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult male bison (YNP 11661) Condylolbasal length, 519 mm. Photographs by A. Vanderbilt.

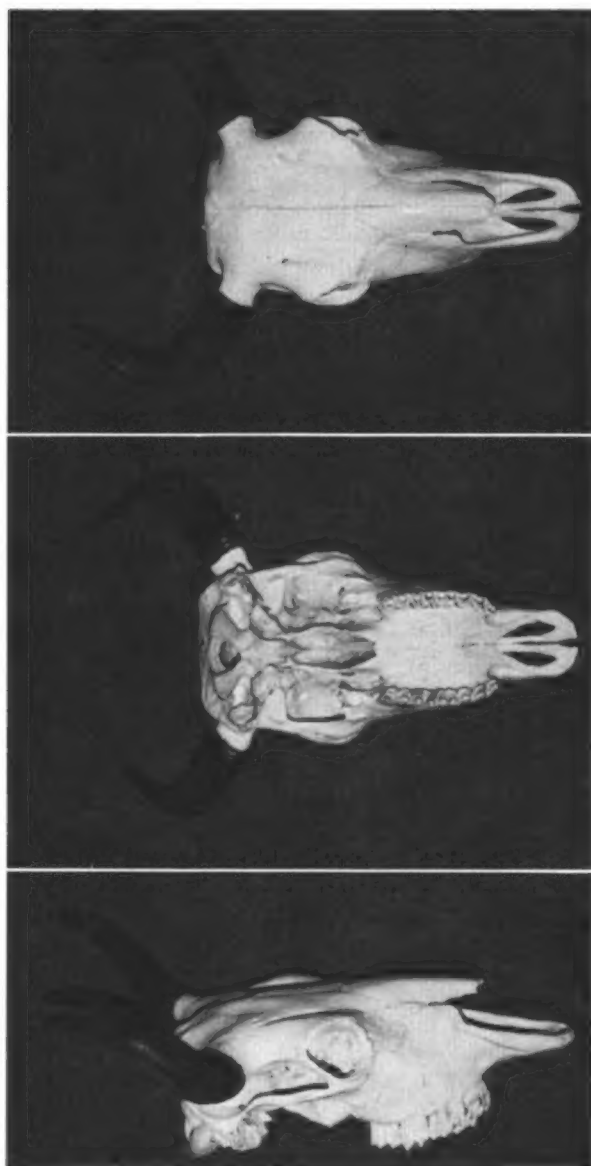


FIG. 2. Dorsal, ventral, and lateral views of cranium of adult female bison (YNP 12050). Condylolbasal length, 460 mm. Photographs by A. Vanderbilt.

Bos-Bison group of Bovini (McDonald, 1981). *Leptobos*, appearing later in the Pliocene and widely distributed in central and southern Eurasia during both the Pliocene and Pleistocene, may be either a common ancestor (Guthrie, 1980; McDonald, 1981) or a closely related taxon (McDonald, 1981). *B. sivalensis*, the earliest known species and possible ancestor of later lineages of bison, dispersed northward into Siberia by the middle Pleistocene or earlier (McDonald, 1981). This species and another poorly known early form, *B. paleosinensis*, seem to have been small bodied, small horned, and more cattle-like compared to later bison, and were probably adapted to a woodland-parkland environment (Guthrie, 1980).

Early in the middle Pleistocene the so-called steppe bison, *B. priscus* appeared (Guthrie, 1980). This larger bodied, larger horned bison apparently was the dominant form during the rest of the Pleistocene and may be ancestral to the North American forms (Guthrie, 1980; Wilson, 1975).

By the late Illinoian to early Sangamon the large steppe bison seems to have spread into the grasslands of central North America where they became even larger, with enormous horn cores reaching 2 m tip to tip (Guthrie, 1980). This form, *B. latifrons* or *B. priscus latifrons*, occurred in much of unglaciated North America but seems to have been most common from Alberta to Texas along the east front of the Rocky Mountains and the intermontane basins. Guthrie



FIG. 3. Photographs of a fully mature male (top) during rut and female (bottom) bison showing contrast in head and horn shape. Photographs courtesy of A. Stephen Johnson.

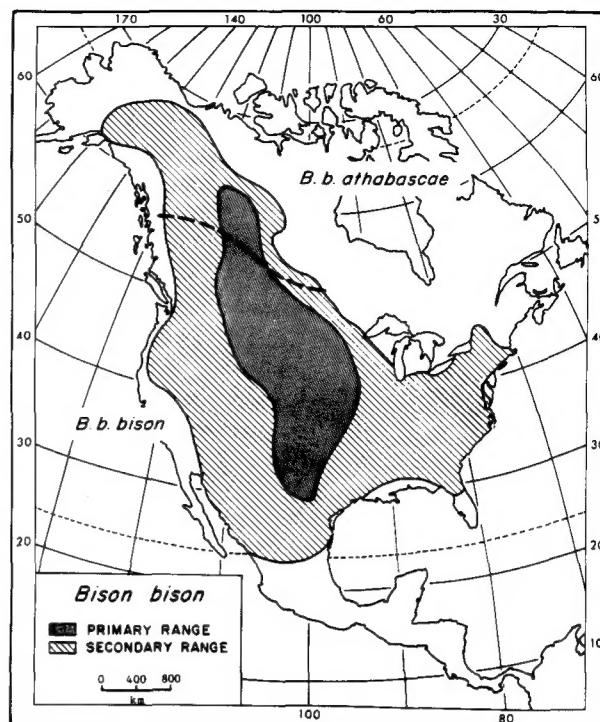


FIG. 4. Map illustrating probable maximum distribution of *B. bison* during late prehistoric times with the north-south axis of the primary range coincident with the central North American grasslands. The maximum extent of the range of *B. b. athabasca* is not as well known as that of *B. b. bison*. Map is fig. 23 from McDonald (1981) courtesy of University of California Press (scale added).

(1980) and Wilson (1975) believed this line decreased in size during the Wisconsin, grading eventually into the smaller *B. antiquus*.

About 13,000–12,000 BP, a gradual diminution in size of *B. priscus* seems to have occurred in the far north (Guthrie, 1980) leading to *B. occidentalis* (Guthrie, 1980; Wilson, 1975). At the end of the Wisconsin, this northern line of *B. occidentalis* may have reinvaded the grasslands of the Great Plains to contact and interbreed with the more southern line of *B. antiquus* (Wilson, 1975). At this time the two lines may have been similar in size although somewhat different in cranial and horn-core morphology (Guthrie, 1980). During the Holocene, North American bison seemingly continued to diminish in body size while at the same time increase in numbers (Guthrie, 1980).

Guthrie (1980) pointed out that the rapid rate of bison evolution led to a bewildering assortment of taxonomic designations. The trend in recent years has been to synonymy (Guthrie, 1980; McDonald, 1981; Skinner and Kaisen, 1947; Wilson, 1975), but temporal and spatial trends seem to warrant subspecific status for resulting differences of form. In this view, then, the evolution of North American bison led to two Holocene species, the earlier *B. priscus*, and the extant *B. bison*, with their subspecies (Guthrie, 1980; Wilson, 1975).

FORM AND FUNCTION. The annual pelage molt begins late winter to early spring. Tattered patches of bleached winter hair may cling to the forequarters well into August. New growth is short, somewhat stiff, and nearly black. By late fall the winter coat of woolly underfur with overlying coarse guard hairs is essentially full grown. Head, underparts, flanks, and rear are dark brown, appearing black at a distance. The long woolly hair across the forequarters commonly lightens to bleached tan, most pronounced on older bulls. Usually there is a dark streak down the front of the hump, suggesting a mane, although the hair is scarcely longer than that over the shoulders.

Length of hair (in mm) has been estimated as follows: flanks and rear, 25; rump and hips, 50 to 90; shoulders and hump, 65 to 160; chaps, 150 to 190; and beard, 300 mm (Meagher, 1973; Soper, 1941). On bulls, the hair of the forehead may be 150 to

210 mm, which may compact into a frizzy mat 100 to 130 mm thick at eye level (Lott, 1974). Peters and Slen (1964) found an average density of hair fibers per cm^2 at the midrib of bison calves to be about 2,992 for females and 2,182 for males. The winter pelage of bison showed a greater weight, density, and fineness of hair per unit area compared with that of three breeds of cattle (Peters and Slen, 1964). These pelage characteristics provide high quality insulation, contributing to the observed ability of bison to winter at temperatures well below zero and in areas swept by strong winds (Meagher, 1973, 1976). Christopherson et al. (1979) attributed the observed cold tolerance of 6-month-old bison calves to their heavy hair coat. The bison metabolic rate in still air at -30°C was maintained or reduced, apparently because of decreased physical activity. However, with the addition of wind at -30°C a lower thermally critical zone was reached with a metabolic rate increase from 700 KJ/kg to 950 KJ/kg. In winter, the upper critical temperature apparently was exceeded at 10°C (Christopherson et al., 1979).

The upper limits of physiological heat tolerance in summer apparently have not been determined. However, the historical presence of modern bison in Texas and Mexico (Reed, 1955) suggests that temperatures may not have imposed geographic limits where forage and water were suitable.

Hooves are black, up to 120 to 130 mm in diameter (Murie, 1954) and 133.5 cm^2 insole area (Telfer and Kelsall, 1979). Tongue, lips, and rhinarium are black.

Bison have 31 vertebrae exclusive of the caudals: the atlas, axis, and 5 other cervicals, 14 thoracics, 5 lumbar, and 5 sacral, which are fused into a composite bone. There are 14 pairs of ribs. The neural processes of the second and third thoracic vertebrae are the longest; in large bulls these may extend 450 to 500 mm (Olsen, 1960).

The dental formula is: i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Hall, 1981). Molariform teeth are hypsodont and selenodont. At birth all deciduous teeth are present and covered by a semitransparent membrane that sloughs off during the first days of life (Fuller, 1959). The first permanent tooth, m1, erupts during the first year; by age 5 all teeth are permanent (Fuller, 1959). Age estimates based on wear thereafter are approximate and subjective.

Four inguinal mammae are present. Milk analysis showed 8.9% nonfat solids, 6.3% protein, 2.9% anhydrous lactose, 6.3% fat, 0.3% calcium (Hebbring, 1983).

Bison bulls yielded dressed carcass weights (without hide, head, and entrails) of 52 to 54%, adult cows yielded 54 to 58% (Halloran, 1957). Analysis of muscle from various body parts showed 28 to 35% protein and 0.8 to 5% fat (Johnson and Deethardt, 1980).

Values for selected cellular constituents of adult bison blood ($n = 163$) were: hemoglobin, $16.99 \pm 1.43 \text{ g\%}$; hematocrit (packed cell volume, PCV), $47.11 \pm 4.06\%$; erythrocytes, $10.08 \pm 1.43 \times 10^6/\text{mm}^3$; and leucocytes, $8.03 \pm 1.41 \times 10^3/\text{mm}^3$ (Mehrer, 1976). The leucocyte component varied according to diet and season (Keith et al., 1978), and was significantly different between bison under 2 years of age and adults (Marler, 1975). Oxygen-carrying capacity for seven adult bison was 22.2 ml/100 ml; oxygen tension at half saturation (P_{50}) was 32 mm at pH 7.4 and 37°C (Haines et al., 1977). Haines et al. (1977) related this comparatively great oxygen carrying capacity and low oxygen affinity to the frequently observed prolonged running ability of bison.

Values for selected blood chemistry components of adult bison serum ($n = 6$) were: total protein, $8.0 \pm 0.6 \text{ g/100 ml}$; globulin, $4.9 \pm 0.2 \text{ g/100 ml}$; bilirubin, $0.7 \pm 0.2 \text{ mg/100 ml}$; blood urea nitrogen, $16.3 \pm 4.1 \text{ mg/100 ml}$; creatinine $2.3 \pm 0.6 \text{ mg/100 ml}$; glucose, $77.5 \pm 9.7 \text{ mg/100 ml}$; cholesterol, $76.0 \pm 8.2 \text{ mg/100 ml}$; calcium, $10.4 \pm 1.0 \text{ mg/100 ml}$; chloride, $113.3 \pm 5.9 \text{ meq/l}$; phosphorus, $5.8 \pm 1.0 \text{ mg/100 ml}$; potassium, $4.2 \pm 0.6 \text{ meq/l}$; sodium, $145.0 \pm 1.8 \text{ meq/l}$; alkaline phosphate, $21.0 \pm 8.6 \text{ U/l}$; lactic dehydrogenase, $545.8 \pm 149.5 \text{ U/l}$; and serum glutamic oxalacetic transaminase, $57.0 \pm 24.8 \text{ U/l}$ (Keith et al., 1978). Schaefer et al. (1978) found mean plasma T_3 and T_4 levels of 45.5 ng/100 ml and 5.42 ng/100 ml , respectively. Blood urea nitrogen was 20.63 mg/dl and 12.33 mg/dl on high-N and low-N diets, respectively (Keith et al., 1981). High- ($D > 1.063$) and low-density ($D < 1.063$) lipoproteins comprised 64 and 36%, respectively, of bison serum total lipids from two heifers (Evans, 1964). Most serum components showed significant variation according to diet quality and time of year (Keith et al., 1978).

Mean heart rate for bison was 89 beats/min; rate fluctuated

as much as 50% within 30 sec (Hawley and Peden, 1982). Mean body temperature was 38.7°C (Hawley and Peden, 1982). Christopherson et al. (1979) recorded mean respiration rates that ranged from 11.2 ± 2.9 to $20.0 \pm 8.8/\text{min}$.

Bison have the ruminant digestive system with a four-compartment stomach consisting of the rumen, reticulum, omasum, and abomasum. Voluntary feed intake in $\text{kg kg body mass}^{-1}\text{day}^{-1}$ by bison was 0.009 on sedge and 0.011 on grass (Richmond et al., 1977).

During rumination a bolus may be chewed 38 to 70 times at a rate of about one chew/s (Fischer, 1967). Pearson (1967) found that rumen microorganisms included eight species of ciliate protozoa and five morphological types of bacteria, with average total counts of $0.58 \times 10^6/\text{ml}$ and $7.14 \times 10^6/\text{ml}$, respectively. Rumen content lipids contained 4, 16, 17, 22, and 33%, respectively, of monoglycerides, triglycerides, sterols, phospholipids, and nonesterified fatty acids (Evans, 1964). Apparent digestibility in percent of a sedge hay diet was: dry matter, 51.3; crude protein, 38.3; crude fat, 64.2; neutral detergent fiber, 54.7; acid detergent fiber, 47.0; hemicellulose, 67.1; lignin, 25.2; and gross energy, 50.6 (Hawley et al., 1981a). On this diet, bison showed an average daily gain in kg/day of 0.42 and 0.04 for summer and winter, respectively. When compared with cattle, digestibility coefficients for all nutrients in low quality (low protein, high fiber) diets were higher, as were digestibilities of various native forages (Hawley et al., 1981b). Rumen ammonia concentrations and urinary urea levels appeared to be proportional to dietary N levels (Keith et al., 1981). Apparent absorption of N from the gastrointestinal tract was 3.50 g/100 g of dry matter; retention time of digesta in feeding trials was 78.8 h (Schaefer et al., 1978).

Droppings are similar to those of cattle. On succulent feed, a flat mass of 30 cm diameter is common; with drier feed a more rounded, layered mass forms (Murie, 1954). Defecation rates of approximately once per h were observed in bulls (Herrig and Haugen, 1969).

The mean brain weight for four subadult males and two mature females was 458 g. Mean forebrain measurements (in mm) were: length, 114.3; width, 93.3; height, 64.1. Mean cerebellum measurements were: length, 44.8; height, 38.7 (Harper and Maser, 1976).

In 4.5-year-old bison the mean chest height for males ($n = 95$) was $677 \pm 3.3 \text{ mm}$ and for females ($n = 23$) was $643 \pm 7.0 \text{ mm}$; the mean foot load, in gm/cm^2 , was 884.1 ± 8.02 and 672.4 ± 9.47 for males and females, respectively (Telfer and Kelsall, 1979). These authors suggested that males might cope more successfully with increased snow depth, but that females might have a greater advantage when walking on hard or dense snow. The musculature of the neck and shoulders allows bison to forage by swinging the head from side to side to clear feeding areas. Mixed groups regularly foraged in snows 600 mm deep, bulls to 900 mm deep (Houston, 1982). McHugh (1958) observed some bison to forage at 1,200 mm.

ONTOGENY AND REPRODUCTION. A few precocious female bison first conceive as yearlings but sexual maturity most commonly occurs at 2 to 4 years of age (Fuller, 1962; Halloran, 1968; Meagher, 1973). Sexual maturity in males is similar. A few show sperm in the epididymis as yearlings; by age 3 most males are sexually mature (Fuller, 1962; Shult, 1972). Although Halloran (1968) found that 2-year-old males might perform effectively as sires in the absence of older males, bulls usually do not breed cows until age 6 (Herrig and Haugen, 1969; Lott, 1981; McHugh, 1958).

The breeding season may extend from late June or early July through September (McHugh, 1958; Meagher, 1973; Shult, 1972) but actual breeding is more strongly seasonal. Lott (1981) reported that about 90% of copulations occurred in a 2-week period with 17 of 37 observed occurring 30–31 July and 1–2 August. Haugen (1974) calculated that most conceptions occurred between 21 July and 19 August with a peak about 1 August. In the north, at Wood Buffalo National Park, breeding activity may begin later (Soper, 1941) and peak between 10 and 20 August (Fuller, 1962).

Gestation was estimated at 285 days (Haugen, 1974). The calving season generally extends from mid-April through May with births often concentrated from the end of April through the first two weeks of May (Lott and Galland, 1985; McHugh, 1958; Meagher, 1973; Rutberg, 1984; Shult, 1972). Out-of-season births are

recorded in most herds, usually later in summer (Fuller, 1962; Lott and Galland, 1985; McHugh, 1958; Meagher, 1973).

Bison cows have one calf; twins are known but are rare (Engelhard, 1970; Fuller, 1962; Halloran, 1968; Haugen, 1974; McHugh, 1958; Roe, 1970). At birth, the calf may weigh 15 to 25 kg (Rutberg, 1984). The fetal sex ratio usually favors males (Fuller, 1962; Haugen, 1974; McHugh, 1958; Meagher, 1973).

Calves are usually bright reddish tan, although Engelhard (1970) recorded some calves with atypical dark streaking and areas of gray. Calves begin to darken to a brownish black at about 2.5 months (McHugh, 1958); darker hair appears first on the head, then the shoulders and back, but calves are not uniformly dark until 4 months (Engelhard, 1970). Sexes are alike in appearance at birth, with no apparent hump. There is a tendency for males to develop slightly larger body size, larger hump, and longer more conical horns by the end of the first year (Engelhard, 1970). Calves usually weigh between 135 and 180 kg by 8 to 9 months of age; yearlings (20 to 22 months) weigh between 225 and 315 kg (Meagher, 1973).

Calves are precocious; average times for 10 calves to first stand and first nurse were 10.9 min and 32.2 min, respectively (Lott and Galland, 1985). They may try to graze by 5 days of age (Shult, 1972) and will drink water after the first week (Engelhard, 1970; Shult, 1972). Engelhard (1970) noted a 1-month-old calf with partly digested grass in the abomasum; calves orphaned at 7 to 8 weeks of age have survived (Shult, 1972). Cows nurse their calves for at least 7 to 8 months (McHugh, 1958), but most calves apparently are weaned by the end of the first year (Halloran, 1968; McHugh, 1958; Shult, 1972; Van Vuren, 1979).

Age of physical maturity in bison apparently differs between the sexes. Bulls appear to attain near-maximum mass by age 5 or 6 with small increments thereafter (McHugh, 1958). Average mass of 237 known-age bulls suggests that maximum was reached at age 10 to 12; similar data for cows suggests that maximum size might be attained by 3 years of age (Halloran, 1968). Horn development provides a rough estimate of maturity for bulls; mature curve and thickness was attained by 7 to 8 years (Fuller, 1959). Cows attain full curvature by 3 to 5 years of age (McHugh, 1958).

Females may be seasonally polyestrous, with a cycle of approximately 3 weeks (Fuller, 1962). Estrus may last 9 to 28 h (Haugen, 1974).

Average longevity in bison has not been documented. Fuller (1959, 1962) placed the onset of old age at 12 to 15 years. In the wild, a few bison apparently survive more than 20 years (Meagher, 1973); records of a few known-age cows of 40+ years were cited by McHugh (1958).

ECOLOGY. An estimated 30 million bison inhabited North America about the time modern man arrived (McHugh, 1972). Subsequently, bison nearly were exterminated through overhunting. Various writers have chronicled this exploitation (Dary, 1974; Haines, 1970; McHugh, 1972; Roe, 1970). By 1903, a known 1,644 bison existed (Garretson, 1938), mostly in zoos and privately owned herds. They survived near extermination as a wild species in two areas: Wood Buffalo National Park, Canada (Soper, 1941), and Yellowstone National Park, Wyoming (Meagher, 1973). Through establishment of additional public preserves and privately owned herds, bison numbered an estimated 75,000 in 1983 (Jennings and Hebring, 1983).

Prehistoric distribution occurred primarily on the central grasslands and northern parklands of North America, but habitats used ranged from semidesert to boreal forest where suitable grazing was available (McDonald, 1981). Bison are grazers at all seasons, taking mostly grasses and sedges (*Carex* spp.). Use of warm season grasses predominated in shortgrass pasture (Peden et al., 1974); cool season grasses including some sedges composed 79 to 96% of the diet of herds on mixed prairie (Popp, 1980). In a shrub-steppe habitat, 96% of the summer diet was grasses (Van Vuren, 1984). Sedges were selected throughout the year in montane and northern areas where sedge-grass meadows are a major habitat component (Meagher, 1973; Reynolds et al., 1978; Soper, 1941; Telfer and Cairns, 1979). Bison ingest an average of 7.4 kg of sedge hay/day (Hawley et al., 1981b), or a mean daily dry matter intake of 1.6% of body mass both summer and winter (Hawley et al., 1981a). Most apparently ingest water or snow daily (McHugh, 1958).

Where bison coexist with other ungulates, interspecific competition apparently is minimized through differences in habitat use

and food habits (McCullough, 1980), and morphology (Houston, 1982; Telfer and Kelsall, 1984). In a shrub-steppe habitat, bison were frequently at higher elevations, generally moved further from water, and grazed steeper slopes than cattle (Van Vuren, 1979). Bison and pronghorn showed spatial overlap but quite different food habits (McCullough, 1980; Wydeven and Dahloren, 1985). The existence of prairie dog (*Cynomys* sp.) towns apparently facilitated bison habitat selection for a shortgrass successional state in a mixed-grass community (Coppock et al., 1983). Among four species of ungulates on a shortgrass pasture, bison were the least selective and ingested the lowest quality forage (Rice et al., 1974; Schwartz and Ellis, 1981). In montane habitat in winter, bison appeared more restricted than elk (*Cervus elaphus*) to highly productive wet meadows where they could forage in deeper snow while obtaining a large quantity of food (Houston, 1982). In boreal forest-aspen-meadows of Elk Island National Park, elk and bison in winter overlapped most in habitat use but least in food habits; the reverse was true in summer (Telfer and Cairns, 1979). Telfer and Kelsall (1984) developed a morphological index in combination with behavioral information to evaluate snow-coping ability of eight species of ungulates; bison ranked below all but pronghorn (*Antilocapra americana*).

Use of forested areas appears limited except occasionally for shade, for escape from insects and other disturbances (Fuller, 1962; Meagher, 1973; Soper, 1941), and for shelter during severe winter storms (Fuller, 1962; Soper, 1941). Foraging in more open forest may be relatively frequent (Fuller, 1962; Soper, 1941) or incidental (Meagher, 1973). Extensive forests were traversed between open foraging areas and on seasonal migrations (Fuller, 1962; McHugh, 1958; Meagher, 1973; Soper, 1941).

Most free-ranging bison appear to be seasonally migratory; movements are directional and also altitudinal in some regions (McHugh, 1958; Meagher, 1973; Soper, 1941; Van Vuren, 1983). They moved distances of about 14 to 40 km in montane habitat (McHugh, 1958), and as much as about 240 km in boreal forest-parkland habitat (Soper, 1941). Travel was usually along well-defined travel routes in montane areas from elevations of 1,828 to 3,049 m (Meagher, 1973). In boreal forest-parklands, movements were more fan-like from winter to summer ranges (Soper, 1941). Apparent influences on seasonal migrations included supply and accessibility of forage (Soper, 1941), spring weather conditions and temperatures, and fall snow storms at higher elevations (Meagher, 1973).

In smaller preserves, bison may have individual but overlapping home ranges. On Santa Catalina Island, 16 bison cows had average home ranges of 56.1 km², ranging from 26.9 to 70.5 km² (Lott and Minta, 1983a); in the Henry Mountains, Utah, six cows had average home ranges of 52 km² (Van Vuren, 1983). Factors which appeared to influence home-range size were plant productivity (Lott and Minta, 1983a; Van Vuren, 1983), environmental homogeneity, and size of preserve (Lott and Minta, 1983a).

Daily movements of bison herds between foraging sites in summer are usual (McHugh, 1958). These averaged 3.2 km in a montane valley (McHugh, 1958) and 2.8 km in coastal scrub-grassland on Santa Catalina Island (Lott and Minta, 1983a). In shrub-steppe habitat the average stay in one area was 1.9 days (Van Vuren, 1979). Apparent influences on summer range movements are seasonal vegetation changes, interspersions and size of forage sites, the rut, and the presence of biting insects in large numbers (Meagher, 1973). Size of preserve and availability of water may be additional influences (McHugh, 1958).

Population structures for free-ranging herds of Wood Buffalo National Park, Henry Mountains (Utah), and Yellowstone National Park, respectively, were: calves, 16, 21, and 22%; yearlings, 9, 13, and 17%; 2- and 3-year olds, 15, no data, and 16%; cows, 39, 36, and 28%; and bulls, 21, 30, and 16% (Fuller, 1960; Meagher, 1973; Van Vuren, 1979). Productivity for females 2.5 years and older was 53, 60, and 52%, respectively. A sub-population with a relatively younger age structure showed productivity of 76% (Fuller, 1962). The proportion of calves in mixed herds in a stable population may be 18 to 20%; 25% may be more usual in a population undergoing increase (Meagher, 1973). Percent composition of calves may be consistent during the first year of life (Meagher, 1973), or may decline June to December at about 2% per month (Fuller, 1962). Recruitment may occur as yearlings (Fuller, 1962), or after the second year (Meagher, 1973). In all three of the foregoing populations, adult males appeared to outnumber adult females.

Mortality in most herds is man-caused through commercial and sport harvest, or subsistence hunting. The wolf (*Canis lupus*) is apparently a competent predator of free-ranging bison. Bison contributed about 65% to the winter diet of wolves in Wood Buffalo National Park, but wolves did not appear to have a negative impact on the bison population (Fuller, 1962). However, wolf and human predation may be additive. On the Slave River lowlands a severe winter coupled with the combined predation apparently triggered a decline in bison numbers from 1,900 to 1,250; bison declined further to about 750 (Reynolds et al., 1982). Bison separated from herds appeared to be the primary targets of attack (Haynes, 1982).

Periodically, severe winter weather is the primary mortality agent in Yellowstone National Park; winterkill to some degree occurs every year with differential mortality among age and sex classes (Meagher, 1973). Unusually severe spring storms may cause both high calf mortality and increase adult mortality (Meagher, 1976). Winterkill also occurs frequently in and adjacent to Wood Buffalo National Park (Reynolds et al., 1982). Accidents are usually insignificant but several thousand bison have drowned in single occurrences (Reynolds et al., 1982).

At least 31 endoparasites have been reported from bison, mostly from captive herds where confinement may enhance occurrence. Effects in wild bison appear insignificant; only 2 of 26 species of nematodes were reported from free-ranging herds: the lungworm, *Dictyocaulus* sp., and the coelomic worm, *Setaria* sp. (Reynolds et al., 1982).

Anthrax outbreaks cause sporadic but appreciable mortality in northern bison. Tuberculosis may affect as much as 50% of the bison of Wood Buffalo National Park but effects of the disease on the population remain obscure. Brucellosis occurs at varying rates, sometimes more than 50% (Reynolds et al., 1982); it may cause abortions but does not appear to prevent population increases (Meagher, 1973). Economic concerns of the cattle industry dictate that most bison herds are maintained brucellosis-free. Chronic fluoride toxicosis is prevalent in geothermally active parts of Yellowstone National Park (Shupe et al., 1984). Other pathological conditions occur infrequently (Reynolds et al., 1982).

BEHAVIOR. Bison are gregarious, forming herds according to sex, age, season, foraging conditions, and habitat. Females of all ages, calves, most males 2 to 3 years old, and one to a few older males form mixed (sometimes called cow) groups throughout the year (Fuller, 1960; McHugh, 1958). Older males join these groups in increasing numbers as rut approaches (McHugh, 1958), but are afterwards found singly, in pairs, or in bull groups containing as many as 30 individuals (Fuller, 1960). Mixed herds are fluid and variable in size but tend to be larger during rut (Lott, 1981) and in more open habitat (Van Vuren, 1983). In spring, cows with calves tend to cluster (Rutberg, 1984). Solitary bulls sometimes rejoin mixed herds (Fischer, 1967; Herrig and Haugen, 1969). Fuller (1960) found that only 34% of lone bulls were 7 years or older. Mixed groups show a high degree of cohesion, and bulls, low levels (McHugh, 1958). However, the cow-calf bond appears to be the only stable relationship (Lott and Minta, 1983b; Van Vuren, 1983).

Cows usually give birth in isolation where vegetation provides cover; where cover is lacking, isolation is infrequent (Lott and Galland, 1985). Parturition for 16 cows averaged 68 min after the amnion became visible (Lott and Galland, 1985). At first the cow-calf association is close with cows often keeping themselves between the newborn and other bison (McHugh, 1958), but by 2 to 3 weeks of age calves often cluster in groups of 2 to 15 (Engelhard, 1970; McHugh, 1958). Mothers commonly defend young calves from perceived danger; bulls were not observed to do so (McHugh, 1958). Adoptions have occurred, but are rare (Engelhard, 1970).

Lott (1981) classified bison as promiscuous but breeding occurs in a one-to-one relationship termed tending, which is initiated by the bull. Copulation is brief. Interaction among mature bulls during the rut is intense; much of it is stylized with threat displays and signals of submission (Lott, 1974; McHugh, 1958). Fights tend to occur in clusters which Lott (1974) termed fighting storms; such fights often terminate without damage but injuries and occasional fatalities occur. Wallowing and tree horning, more commonly done by bulls, increase during rut.

Dominance between bulls generally is linear but reversals may occur (Lott, 1979b). Aggressive interactions between bulls, rather than age and weight, apparently confer status, and bulls with high status have higher breeding rates (Lott, 1979b). The copious display

hair of head, beard, and chaps of mature bulls apparently decreases from physiological changes after rut; this may decrease postrut aggression and attendant energy costs (Lott, 1979a). Cows also show linear dominance but reversals are rare; Rutberg (1983) suggested that female status is established early between individuals and seldom contested during their lifetimes.

Bison are primarily diurnal, with several grazing periods interspersed with loafing and ruminating (McHugh, 1958; Shult, 1972). Grazing occurs in a loose grouping that Shult (1972) termed a wave pattern, but travel is usually in line and is influenced by terrain and habitat conditions. Leadership is usually by an adult cow, but not necessarily by the same individual on all occasions (McHugh, 1958).

McHugh (1958) described gaits as walking, trotting, galloping, and bounding. Speeds of nearly 60 km/h may be attained in spurts. Bison are strong swimmers; Fuller (1960) noted that bison regularly swam rivers approximately 1 km wide with currents of perhaps 3 to 6 km/h.

Smell is acute and appears to be important in detecting danger (Fuller, 1960; McHugh, 1958). Flehmen (lip curl) occurs generally but is most commonly seen in mature bulls during rut, when it may facilitate identification of a cow in estrus (Lott, 1981). Hearing is acute. Bison may visually distinguish large objects such as a horse with rider at about 1 km, and moving objects at nearly 2 km (McHugh, 1958). Vocalizations commonly consist of grunts and snorts audible at short distances; the distinctive roar or bellow of rutting bulls may carry nearly 5 km (McHugh, 1958).

GENETICS. The diploid number is 60; there are 29 pairs of acrocentric autosomes, a metacentric X- and a small acrocentric Y-chromosome (Basrur and Moon, 1967; Bhambani and Kuspira, 1969). Ying and Peden (1977) indicated that at least 20 pairs of autosomes and the sex chromosomes of *B. b. athabasca* and *B. b. bison* are homologous. The autosomes and the X-chromosome of *B. bison* are indistinguishable from those of *Bos taurus*. Cross-breeding experiments between bison and cattle date back apparently to the 1700's (Dary, 1974; Haines, 1970; McHugh, 1972; Roe, 1970) and continue to the present. Bison bull matings with cattle females generally result in fatalities to cow and calf because of excess amniotic fluid. Female hybrids are fertile, males are not.

Polymorphism in components of bison blood has been distinguished as follows: hemoglobin, two (Harris et al., 1973); 6-phosphogluconate-dehydrogenase, three (Naik and Anderson, 1970); and carbonic anhydrase, five (Sartore et al., 1969). Albinism occurs in bison, but rarely (McHugh, 1958; Roe, 1970).

REMARKS. The taxonomic status of *B. b. athabasca* and *B. b. bison* remains somewhat controversial. The differences in shape and pelage described by Geist and Karsten (1977) may be modified as larger samples are compared. Studies of chromosomes (Ying and Peden, 1977) and blood characteristics (Peden and Kraay, 1979) have not resolved the issue.

Additional research needs on bison include further anatomical and physiological descriptions and comparisons with wisent and cattle, further studies of adaptive strategies and interspecific relationships, and long-term analyses of the population dynamics and factors that naturally regulate the different free-ranging populations. Additional behavioral studies that compare various populations would be useful. Researchers and non-researchers alike would benefit from further studies of the evolutionary history and more recent forms of bison that might allow a consensus on nomenclature and the species and subspecies represented.

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